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Growth and Reproduction of Benghal Dayflower (*Commelina benghalensis*) in Response to Drought Stress

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Greenhouse experiments were conducted to evaluate growth and reproduction of Benghal dayflower in response to daily (nondrought stress) and weekly (drought stress) irrigation. With daily irrigation, Benghal dayflower plants added one leaf per plant each week during the initial 6 wk of growth and then increased leaf number eightfold between the intervals of 6 and 10 wk after planting (WAP) and 10 and 15 WAP. By 15 WAP each plant had in excess of 400 leaves. Benghal dayflower plant height increased 2.4 cm wk^{-1} between 5 and 14 WAP, increasing eightfold during this interval, while plant width increased 20-fold. Aerial spathe formation began between 7 and 8 WAP, with 26 spathes maturing (containing seeds ready for dispersal) each week beginning at 11 WAP. In another study, the influence of duration of drought stress at intervals between 7 and 56 d on early growth and development of cotton and Benghal dayflower was evaluated. Benghal dayflower aboveground biomass was 3.5 times greater than cotton. There was an inverse linear relationship between aboveground biomass and duration of drought stress for cotton and Benghal dayflower, though there was a more rapid decline for Benghal dayflower. A final study evaluated Benghal dayflower response to weekly moisture regimes that approximated 13, 25, 50, and 100% of soil field capacity. Benghal dayflower aerial spathes were 4.6 times more numerous than subterranean spathes. Rate of seed production decreased in a linear manner with decreasing water volume, however, rate of subterranean seed production was less affected by water volume than was aerial seed production. These data indicate that Benghal dayflower thrives under high soil moisture regimes, but that drought stress inhibits growth and reproduction. Cotton appears to be more drought tolerant than Benghal dayflower. Judicious water use in cotton cropping systems in the southeastern United States could be an important component of multiple-tactic Benghal dayflower management program.
Nomenclature: Benghal dayflower, *Commelina benghalensis* L. COMBE; cotton, *Gossypium hirsutum* L.
Key words: amphicarpic species, chasmogamous flowers, cleistogamous flowers, tropical spiderwort, weed seed production.

Benghal dayflower (also known as tropical spiderwort) is an important weed species in Africa and Asia, especially in irrigated fields (Budd et al. 1979; Chivinge and Kawisi 1989; Kaul et al. 2002; Wilson 1981). This species is an exotic, invasive weed that is also listed on the U.S. Federal Noxious Weed List. *Commelina* species were not included among the most common or troublesome weeds of cotton in Georgia in 1974, 1984, or 1995 (Buchanan 1974; Dowler 1995; Elmore 1984). A survey of county agents in Georgia following the 1998 growing season indicated that *Commelina* species were considered troublesome in several crops, but were ranked as the 39th most troublesome weeds when averaged across all cropping systems (Webster and MacDonald 2001). In 2001, *Commelina* species were ranked as the ninth most troublesome species of cotton and by 2005 Benghal dayflower was the most troublesome species (Webster 2001, 2005). Many factors have contributed to the rapid increase in importance of Benghal dayflower in Georgia cotton agroecosystems, including the tolerance of Benghal dayflower to glyphosate, widespread use of glyphosate in glyphosate-tolerant cotton, and reductions in use of cultivation and preemergence herbicides, two tactics which previously suppressed Benghal dayflower growth (Culpepper et al. 2004; Prostko et al. 2005; Webster et al. 2005a, 2006).

Soils in the Coastal Plain of the southeastern United States are typically coarse textured (i.e., loamy sands or sandy loams) with low amounts of organic matter (<1%) and limited water-holding ability (USDA-NRCS 1999). As a result, supplemental irrigation is an important component of many agroecosystems in this region. Rising fuel costs and limited water availability may reduce the frequency or possibility of supplemental irrigation, potentially resulting in greater drought stress for crops and weeds. In general, *Commelina* species are often associated with low-lying, moist areas within agricultural fields (Holm et al. 1977; Wilson 1981). However, Benghal dayflower has moved from the ditch-banks at the field margins and low areas within a field to become a dominant species distributed throughout production agriculture fields in south Georgia and Florida. A previous study determined that Benghal dayflower growth converted limited water resources into greater biomass than did a similar congener, *C. bracteosa* Hassk. (Burns 2004).

Benghal dayflower is amphicarpic, possessing the ability to produce two types of fruits (aerial and subterranean) with different roles (Maheshwari and Singh 1934; Maheshwari and Maheshwari 1955). Amphicarpy is characterized by two reproductive strategies: (1) one that is successful in a predictable environment in which the plant will have significant vegetative growth prior to abundant fruit production and (2) another in which an unpredictable environment dictates that reproduction occur early in the growing season without regard to maximizing fruit production (Zeide 1978). Aerial seeds of Benghal dayflower are produced by chasmogamous (typical, open pollinated) flowers as part of the reproductive strategy in a predictable environment; while subterranean seeds, formed from cleistogamous (closed, self pollinated) flowers, ensure reproduction in an unpredictable environment. Due to the recent and rapid change in the prominence of Benghal dayflower in agricultural production in the southeastern United States, little information exists concerning the physiological responses of this weed to drought stress. Therefore, the objectives of these studies were to evaluate growth and reproduction of Benghal dayflower in response to daily (nondrought stress) and weekly (drought stress) irrigation.

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Materials and Methods

Benghal Dayflower Growth Without Drought Stress. Greenhouse studies were planted in February 2004 and 2005 to evaluate Benghal dayflower growth and reproduction under daily irrigation. Seeds were scarified using a razor blade and planted into pots (30 cm in diameter and 15 cm deep) filled with Tifton loamy sand (87% sand, 7% silt, 6% clay; fine-loamy, kaolinitic, thermic, Plinthic Kandiudult) with pH of 6.3 and 0.8% organic matter. Once emerged, plants were thinned at the cotyledon stage to one plant per pot. In both years, the growth of 10 plants was evaluated over a 20-wk period. Pots were irrigated at least daily so that water was not limited. Each week, the numbers of leaves per plant, plant height, plant width, and number of mature aerial spathes were determined. Plant height was measured from the soil surface to the position of the highest leaf. Plant width was measured as the average of the plant diameter at the widest point and the measurement at 90 degrees to that point. Benghal dayflower growth data were regressed on time and fit to sigmoid regression models. Regression models were fit to all data, but treatment means and standard errors were presented for clarity.

Benghal Dayflower and Cotton Growth under Drought Stress. Greenhouse studies were initiated in July 2005, June 2006, and August 2006 in Tifton, GA. A subsample of soil, previously described in the above experiment, was air dried, sieved (2 mm), and the pH and volumetric water content were determined (Adams et al. 1982). The value of volumetric water content will be referred to as field capacity. Cotyledon-stage Benghal dayflower seedlings were collected from a naturalized population in a farmer's field in Grady County, GA, with GPS coordinates of 30.9915, −84.2921. Each Benghal dayflower treatment consisted of a seedling that was transplanted into previously described pots and soil. Prior to this, cotton ('DP 555 BG/RR') was planted in vegetable seedling trays (128 cells, each cell 3.8 cm wide and long and 6.4 cm deep) and transplanted at the cotyledon stage into pots with a 30-cm diameter and 15-cm depth. Immediately following transplant, all pots were watered with 1500 ml of water (field capacity). Treatments were initiated 1 wk after transplant. Any plants that displayed symptoms of transplant shock at the initiation of the study were excluded from the experiment.

The first drought stress study included treatments of various drought periods: 7, 21, 35, 49, and 56 d. All treatments were watered weekly with 1500 ml at the initiation of the 63 d study and continued to receive this amount of irrigation for the prescribed interval. For example, the 56 d drought interval ceased receiving irrigation on day 7 of the study, while the 21-d drought interval received its final irrigation event on day 42 of the study. Water loss between irrigation events was not restricted. The second drought stress study, which ran concurrent with the first, included four rates of irrigation (188, 375, 750, and 1500 ml), applied weekly to Benghal dayflower for 9 consecutive weeks, which simulated moisture availabilities of 13, 25, 50, and 100% of soil field capacity at the time of irrigation, respectively. Both drought stress studies were arranged as a randomized complete block design with four replications and were repeated over time twice. Data collected in both studies included cotton and Benghal dayflower plant height, plant width, number of leaves per plant, and aboveground dry biomass, as well as number of Benghal dayflower aerial and subterranean spathes and seeds.

Data were subjected to ANOVA. Plant growth parameters were regressed on both water volume and duration of drought stress using a linear regression model. A linear regression model was fit to all data, while treatment means and standard errors are presented for clarity. Due to lack of treatment by study interactions, data were combined over repetitions of the experiments. The rates of growth (slope of the regression) of cotton and Benghal dayflower for common parameters were compared using a *t*-test at an alpha level of 0.05 (Glantz and Slinker 2001).

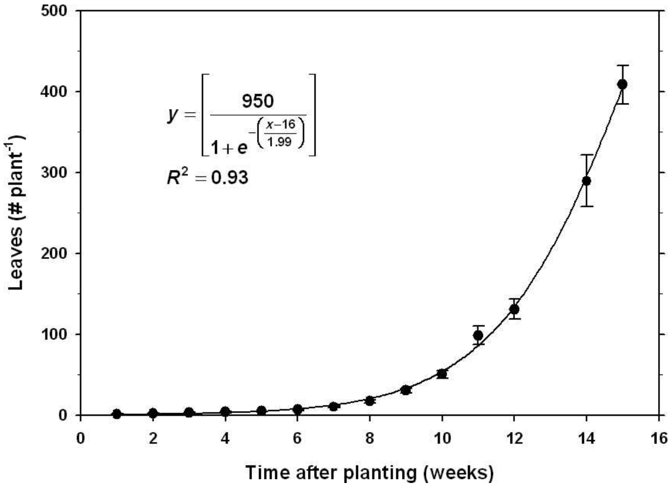

Figure 1. The sigmoid relationship between number of Benghal dayflower leaves per plant under a daily irrigation regime and time. The interval around the treatment means represent the standard error.

Results and Discussion

Benghal Dayflower Growth Without Drought Stress. During the initial 6 wk of the study, Benghal dayflower plants added one new leaf each week (Figure 1). Plants added leaves rapidly over the next 4 wk, increasing leaf number between 6 and 10 WAP by eightfold. By 10 WAP, each plant averaged 50 leaves. The number of new leaves between 10 and 15 WAP increased eightfold, so that by the conclusion of the study, each plant had an excess of 400 leaves.

Benghal dayflower plant height increased in a linear manner over the course of the study (Figure 2). Between 5 and 14 WAP, Benghal dayflower plant height increased at a rate of 2.4 cm wk^{-1}. Benghal dayflower is a decumbent species, but will readily grow vertically if supported by adjacent vegetation. Benghal dayflower may have achieved its maximum height by 14 WAP, as the unsupported vertical growth began a more vine-like growth habit (Figure 3). Over the course of the study, Benghal dayflower plant height increased eightfold, while plant diameter increased 20-fold.

There was a linear relationship between mature aerial spathes and time over the interval of 11 and 20 WAP (Figure 4). The rate of aerial spathe maturation beginning at 11 WAP was 26 spathes wk^{-1}. Under field conditions in its native India, Benghal dayflower aerial flower formation typically begins 8 to 10 wk after emergence (Kaul et al. 2002). In the current study, aerial spathe formation began between 7 and 8 WAP, with immature seed appearing approximately 2 wk later. Kaul et al. (2002) quantified

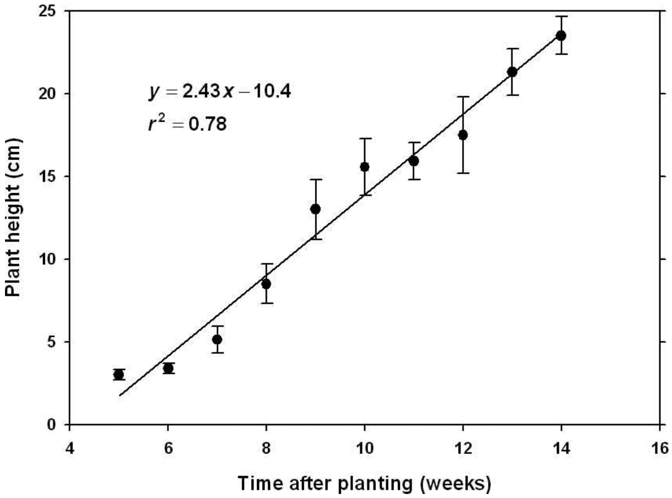

Figure 2. The linear relationship between Benghal dayflower plant height under a daily irrigation regime and time. The interval around the treatment means represent the standard error.

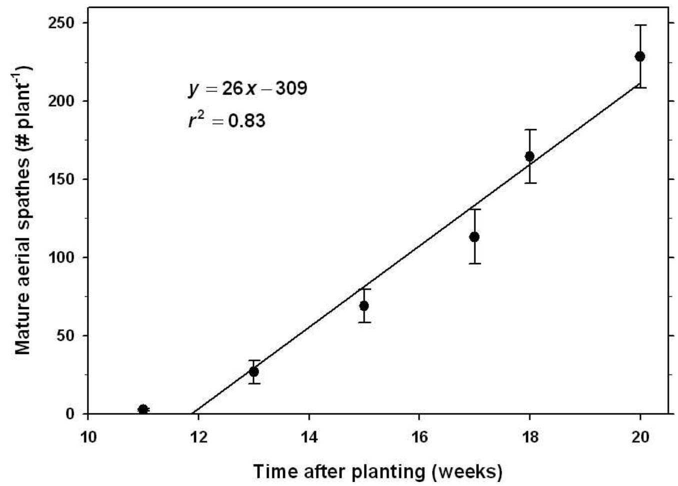

Figure 4. The linear relationship between mature Benghal dayflower spathes under a daily irrigation regime and time. The interval around the treatment means represent the standard error.

spathes of plants in the "flower-fruit stage" and found an average of 99 aerial spathes per plant. By the conclusion of the current study, there were approximately 230 mature aerial spathes on each plant, with an additional 90 immature spathes.

Benghal Dayflower and Cotton Growth under Drought Stress. Benghal dayflower growth was greater than cotton, producing four times more aboveground biomass relative to cotton when both received weekly irrigation to 100% soil field capacity (Figure 5). Similarly, Benghal dayflower growth was greater than cotton in terms of plant width (3.1 times greater), plant height (1.7 times greater), and number of leaves (nine times greater) (data not shown). This reflects the aggressiveness of Benghal dayflower and the relatively rapid growth compared to cotton. This competitive advantage in early season growth supports the reported yield losses from season-long interference of Benghal dayflower, which ranged from 40 to 62% and 51 to 100% yield loss for cotton and peanut (*Arachis hypogaea* L.), respectively (Ahanchede 1996; Webster et al. 2005b, 2007).

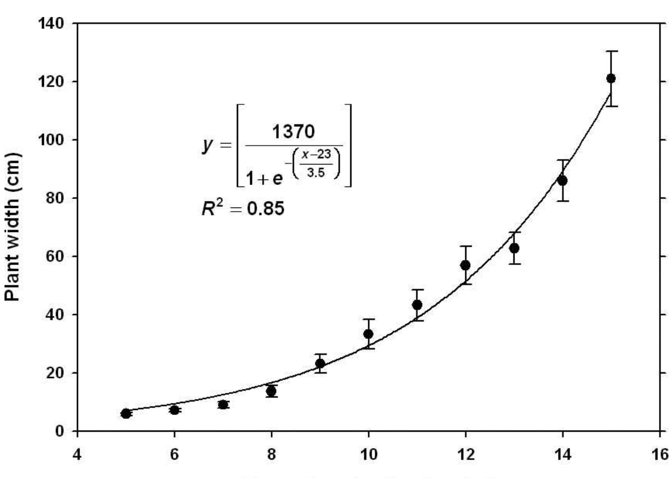

Figure 3. The sigmoid relationship between Benghal dayflower plant width under a daily irrigation regime and time. The interval around the treatment means represent the standard error.

There was an inverse linear relationship between aboveground biomass and duration of drought stress for cotton and Benghal dayflower (Figure 5). The rate of Benghal dayflower biomass accumulation (slope of the regression) was reduced about four times more than rate of cotton biomass accumulation ($t = 6.5_{6df}$). Similar results were observed for the rate of decline in plant width and number of leaves per plant as a function of duration of drought stress, with Benghal dayflower plants affected by drought stress more than cotton plants (Table 1). One mechanism by which cotton plants tolerate drought stress is through establishment of a deep root system. Previous research indicates that a cotton taproot may extend to a depth of 25 cm by the time cotton cotyledons emerge (Ritchie et al. 2007). Pots in the current study had a depth of 15 cm, which may have limited cotton root growth and exacerbated drought stress. The fibrous root system of Benghal dayflower typically remains near the soil surface and was probably not affected by pot depth. However, in spite of this limitation, cotton growth rate was more tolerant of drought stress than Benghal dayflower.

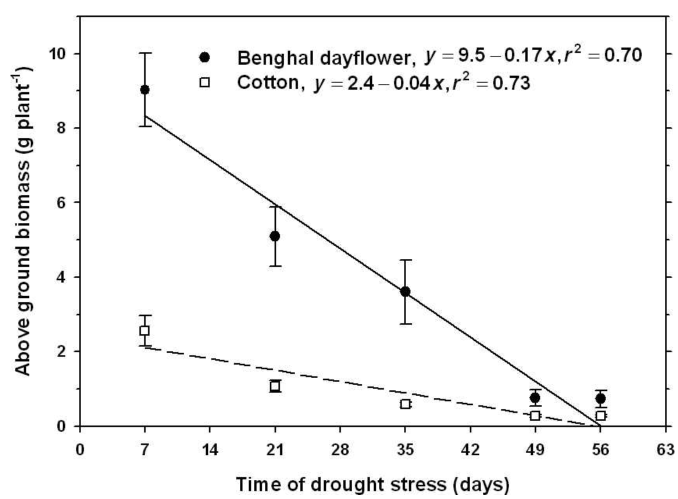

Figure 5. The inverse linear relationship between plant biomass and duration of drought stress for Benghal dayflower and cotton over the 9-wk study. A *t*-test indicated that the rates of biomass accumulation as a function of duration of drought stress for cotton and Benghal dayflower were different ($t = 6.5_{6df}$). The interval around the treatment means represent the standard error.

Table 1. Parameter estimates for linear relationships between plant growth (Benghal dayflower or cotton) and duration of drought stress, with standard error of the mean in parenthesis.

	Benghal dayflower			Cotton			
Parameter	Slope (SE)	r^2	*P*-value	Slope (SE)	r^2	*P*-value	*t*-test[a]
Plant width	−0.70 (0.098)	0.56	< 0.0001	−0.29 (0.037)	0.78	< 0.0001	3.9**
Plant height	−0.44 (0.061)	0.56	< 0.0001	−0.32 (0.045)	0.72	< 0.0001	1.6
Leaves plant^{-1}	−0.93 (0.100)	0.69	< 0.0001	−0.13 (0.013)	0.83	< 0.0001	7.9***

[a] *t*-test compares the slope of the linear regression (growth rate) of Benghal dayflower and cotton, with 6 df.
** P < 0.01.
*** P < 0.001.

The drought stress imposed during this study was harsh, simulating a weekly rainfall/irrigation event. However, in the most frequent irrigation treatment Benghal dayflower growth was similar to that in the study that was irrigated daily. At the conclusion of the drought stress study, Benghal dayflower plants in the most frequent irrigation treatment had 53 leaves and plant height of 22 cm (data not shown), similar to plants of the same age (10 WAP) in the daily irrigation study (Figures 1 and 2). In isolation, a fixed amount of limited water reduced Benghal dayflower growth more than cotton. However, it cannot be ascertained whether these findings would be consistent when cotton and Benghal dayflower were in direct competition for the limited water resource.

In addition to affecting Benghal dayflower and cotton growth, drought stress will also complicate management of Benghal dayflower with herbicides. Increases in leaf cuticle thickness and number of trichomes were observed when Benghal dayflower was subjected to drought stress (25% of field capacity) relative to plants grown at 100% field capacity (Steptoe et al. 2006). At 25% field capacity, the effective herbicide doses increased 2.4 to 250 times for atrazine, flumioxazin, imazapic, 2,4-D, and sulfentrazone relative to the same herbicides applied to plants at 100% of field capacity (Steptoe et al. 2006). Therefore, while early season Benghal dayflower growth will be affected by drought stress more than cotton, control with several herbicides will also be more difficult.

Aerial and Subterranean Reproduction Benghal Dayflower under Drought Stress. Both the aerial seeds (produced by chasmogamous flowers) and subterranean seeds (produced by cleistogamous flowers) were related to irrigation volume in a linear manner (Figure 6) and duration of drought stress in an inverse linear manner (Figure 7). Seed production occurred at the lowest moisture level and was similar for both aerial and subterranean fruits (Figure 6). However, the rate of aerial seed production was 8.6 times greater than subterranean seeds ($t = 4.1_{4df}$), indicating that aerial seed production was more sensitive to relative moisture status than was production of subterranean seeds. Previous research with other amphicarpic species, *Nassella leucotricha* (Trin. & Rupr.) R.W. Pohl, *Collomia grandiflora* Dougl. ex Lindl., and jewelweed (*Impatiens capensis* Meerb.), indicated that cleistogamous reproduction was favored over chasmogamous reproduction as soil moisture became more limited (Brown 1952; Minter and Lord 1983; Waller 1980). Similarly, in the current study as duration of drought stress increased, rate of aerial seed production was reduced more ($t = 4.6_{6df}$) than was subterranean seed production (Figure 7). Subterranean seed production ranged from 1 to 10.3 seeds plant^{-1} at all durations of drought stress, while 49 and 56 d of drought stress prevented aerial seed production (Figure 7). Production of subterranean seeds under all moisture levels ensures survival of the population in an unpredictable environment and contributes to the weedy nature of this exotic species.

Subterranean seeds of amphicarpic plants typically have limited dispersal and are larger than aerial seeds (Kaul et al. 2000). Previous studies determined that subterranean seeds accounted for less than 4% of the total number of seeds produced (Kim 1998; Walker and Evenson 1985). Aerial flower production under field conditions was initiated at the 17- to 19-leaf stage of Benghal dayflower, while subterranean flower initiation occurred at the 7- to 10-leaf stage (Kaul et al. 2002). The short duration of the current study and the relative earliness for subterranean seed production compared to aerial seeds may account for the greater proportion (12%) of the subterranean seeds in this study at the highest irrigation volume compared to previous reports. In addition to producing seeds earlier in the growing season, seedlings produced by the larger subterranean seed of amphicarpic plants are more vigorous and have a greater competitive ability than those produced by aerial seeds (Kaul et al. 2000). Benghal dayflower produces two types of subterranean seeds, large (8.81 mg seed^{-1}) and small (3.51 mg seed^{-1}) (Santos et al. 2001), which are 1.8 to 4.6 times larger than small aerial seeds.

Aerial flowers of amphicarpic plants will produce numerous light-weight seed that are readily dispersed from the parent plant and allows for the possibility of cross-pollination, which encourages adaptability and plasticity within the population (Cheplick 1994; Kaul et al. 2000). Benghal dayflower produces two types of aerial seed, with each flower containing two to four

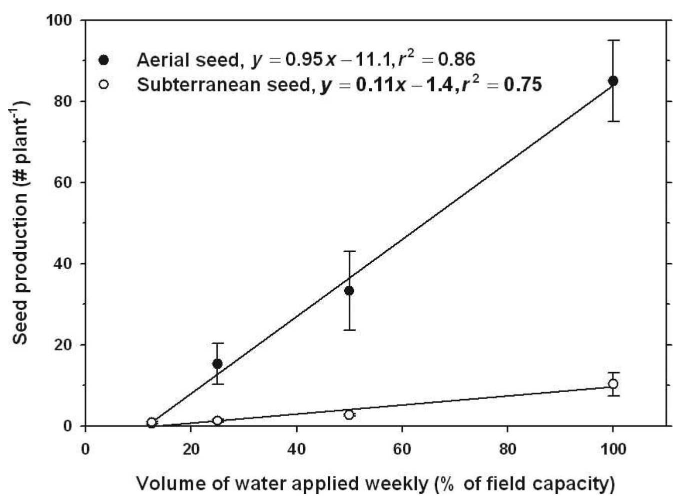

Figure 6. The linear relationship between Benghal dayflower seed production and volume of water applied weekly for aerial and subterranean seeds over the 9-wk study. A *t*-test indicated that rates of seed production as a function of irrigation volume for aerial and subterranean seeds were different ($t = 4.1_{4df}$). The interval around the treatment means represent the standard error.

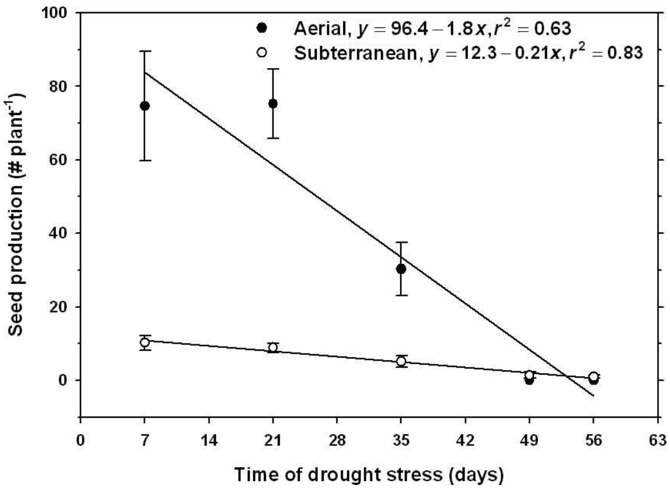

Figure 7. The inverse linear relationship Benghal dayflower seed production and volume of water applied weekly for aerial and subterranean seeds over the 9-wk study. A *t*-test indicated that rates of seed production as a function of duration of drought stress for aerial and subterranean seeds were different ($t = 4.6_{6df}$). The interval around the treatment means represent the standard error.

small (1.9 mg seed^{-1}) seed and one large (3.65 mg seed^{-1}) seed (Faden 1993, 2000; Santos et al. 2001). Birds have been shown to consume aerial seeds, however, it is not known if these seeds can survive the digestive tract (Carter et al. 2006). Aside from human-mediated seed movement (i.e., farm machinery, as contaminants of harvested crops) there are no other obvious means of dispersal for these seed. Gibson and Tomlinson (2002) suggested that the lower competitive ability of smaller seeds in a heterocarpic species may offset greater dispersal ability to new sites compared to larger seeds, which may also be the case with Benghal dayflower. Some of the variability in the current study may be associated with the size (small vs. large) and type of seed (aerial vs. subterranean) that generated the seedling. Seedlings in the nondrought study developed from aerial seeds, both large and small. In the drought stress studies, cotyledon-stage seedlings were collected from a grower's field, therefore we were unable to determine the nature of the seed that produced each seedling.

In terms of implications of these findings for management of Benghal dayflower in the field, this species benefited more than cotton from soil moisture conditions that approached field capacity. The ability to tolerate and even thrive in wetter areas has been documented where Benghal dayflower is a weed in flooded rice (*Oryza sativa* L.) fields (Nandal and Singh 1993; Pancho 1964). In its native habitat in India, Benghal dayflower is a rainy season weed, requiring moist soil conditions for establishment (Kaul et al. 2002). However, once established in moist soil it will migrate to drier areas of a field (Holm et al. 1977). Judicious water use in cotton cropping systems in the southeastern United States could be an important component of a multiple-tactic Benghal dayflower management program due to the differential drought tolerance of these seedlings. Additional research will be necessary to assess the relative water use efficiency of Benghal dayflower and cotton under direct competition.

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